THE JAW APPARATUS OF RECENT *NAUTILUS* AND ITS PALAEONTOLOGICAL IMPLICATIONS

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ABSTRACT. The jaw apparatus of extant cephalopods consists of articulated beak-like mandibles which are composed of chitin and powered by strong buccal muscles. Upper and lower jaws of *Nautilus* possess conspicuous calcite coverings; the upper jaw is characterized by a robust, arrow-shaped calcite element, the rhyncholite; the anterior region of the lower jaw possesses a delicately denticulated calcite element, the conchorhynch. The rhyncholite functions as an incisor operating against the lower cutting edge of the conchorhynch, producing a powerful shearing action. Rhyncholites extracted from the extant species *Nautilus pompilius*, *N. macromphalus*, and *N.* cf. *pompilius* are indistinguishable, in contrast to the conchorhynchs, which are species-distinctive. Both rhyncholites and conchorhynchs range from Middle Triassic to Recent. Circumstantial evidence, including the geologic range, the analogy of *Nautilus*, and the contrasting form of ammonoid and dibranchiate mandibles, indicates that rhyncholites and conchorhynchs belong exclusively to the Nautilaceae. In view of the close similarity between fossil and modern cephalopod jaws, the use of parataxial form genera such as *Rhyncolites* Biguet, 1819 and *Conchorhynchus* de Blainville, 1827 is both practical and necessary for classifying isolated cephalopod jaw elements.

NAUTILUS, the only surviving tetrabranchiate cephalopod, is distinguished from modern dibranchiates by such features as the chambered external shell, the number of gills, and the less complex eye and statocyst. Additionally, *Nautilus* is the only extant cephalopod which secretes calcareous jaw elements (text-fig. 1); the mandibles of octopods, sepiids, and teuthids are composed entirely of chitin and they characteristically have sharper, more saggitate, beaks (text-fig. 2).

Fossil remains of cephalopod jaws, although generally rare, are geographically widespread and well known in rocks of Mesozoic and Cenozoic age. Most commonly encountered as fossils are the isolated, calcified portions of the upper jaw (rhyncholites) and less frequently, the lower jaw (conchorhynchs); the noncalcified chitinous portions of the jaws are very rarely preserved. Rhyncholites and conchorhynchs have been known in the palaeontological literature for over 150 years. Some early authors mistakenly identified them as avian beaks (*fide* d'Orbigny 1825) and cirripeds (von Schlotheim 1820), but their general similarity to modern squid and sepiid mandibles was recognized by Gaillardot (1824) and they were thought to belong to belemnoids by Biguet (1819), de Blainville (1827), and others. Although d'Orbigny (1825) thought they belonged to *Nautilus*, it was not until Sir Richard Owen's memoir on *Nautilus* was published in 1832 that the exact affinity with shelled cephalopods was demonstrated. Additional descriptions of *Nautilus* mandibles have been presented by Foord (1891), Griffin (1900), Willey (1902), Teichert *et al.* (1964), and most recently by Gasiorowski (1973). In spite of the seemingly well-documented status of *Nautilus* mandibles and their fossil counterparts, confusion has persisted regarding the morphology, terminology, and palaeontological implications of the various

elements. The present study is an attempt to clarify these matters, in addition to presenting new data and interpretations.

MATERIAL

We have been fortunate in having had considerable comparative material available for study, including the following:

Nautilus pompilius Linné, 1758 (SUI 42422–42433); ten dried mandibles from Tinaogan Reef, north of Bindoy, Tañon Straits, Negros, Philippines (N. Haven 1971).

Nautilus pompilius Linné, 1758 (DMNH 106740); alcohol-preserved animal from 200 m depth off Medina Point, Gingoog Bay, Mindanao, Philippines (H. K. Dugdale and B. Abrea Jan. 1975).

Nautilus macromphalus Sowerby, 1849 (SUI 42434); two formalin-preserved buccal masses, New Caledonia (A. Bidder).

Nautilus macromphalus Sowerby, 1849 (SUI 35924); formalin-preserved animal, from Baie du Sandal, Lifou, Loyalty Islands ('animal F' of Denton and Gilpin-Brown 1966, p. 729).

Nautilus macromphalus Sowerby, 1849 (SUI 42163, 42164); two alcohol-preserved animals, Nouméa, New Caledonia (Mme. Catala-Stucki, R. A. Davis 1975).

Nautilus cf. *pompilius* Linné, 1758 (SUI 42435–42441); eight alcohol-preserved buccal masses, from 155 m depth off Mutremdiu Point, Uchelbeluu Reef, Belau (Palau) Islands, W. Caroline Islands (D. Faulkner 1976).

For the benefit of future workers, it should be noted that alcohol should be used to preserve the buccal mass instead of formalin, for in all of the formalin-preserved specimens studied, the calcified portions of the mandibles had been partially to completely dissolved.

Materials utilized are reposited at the following institutions (with abbreviations as cited in text): British Museum (Natural History) BMNH; Delaware Museum of Natural History (DMNH); University of Iowa, Department of Geology (SUI).

THE JAW APPARATUS OF *NAUTILUS*

Morphology

The buccal mass of *Nautilus* is covered by a thin, muscular membrane which coalesces with the oesophagus aborally and terminates orally in circlets of buccal papillae surrounding the mouth (Pl. 9, fig. 9). The space within the buccal mass is occupied by more than a dozen separate muscles and by a prominent tongue, which partly bears the large radula. Four fleshy folds, the anterior and posterior prelingual processes of Griffin (1900), project in front and on either side of the anterior portion of the tongue; two additional projections located on both sides of the posterior portion of the tongue bear salivary gland pores.

The jaws, which are enclosed by the buccal membrane, are strong and flexible during life, but rapidly dessicate and become brittle if exposed to air. As in other extant cephalopods, the jaws are composed of chitin. The oral, or biting surface of each jaw is dense and hard, in contrast to the flanks, which are quite flexible. However, infra-red absorption spectra (text-fig. 3) show no compositional differences between different parts of the chitinous jaw. The upper jaw is enclosed within the larger lower jaw (Pl. 9, figs. 7, 8). Each jaw is folded, and thus double-walled, anteriorly. The outer surfaces of both jaws (i.e. those portions in contact with the buccal membrane)

Dorsal

upper jaw

rhyncholite

conchorhynch

anterior   posterior

lower jaw

Ventral
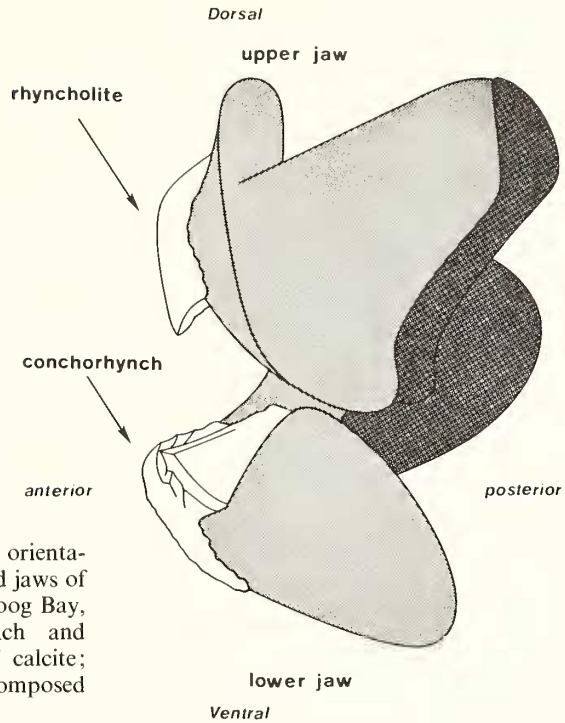
TEXT-FIG. 1. *Nautilus* mandible terminology and orientation. Oblique lateral view based on disarticulated jaws of *Nautilus pompilius* (DMNH 106740) from Gingoog Bay, Mindanao, Philippines (× 1·5). Conchorhynch and rhyncholite (both in white) are composed of calcite; the other portions of the mandibles (stippled) are composed of chitin.
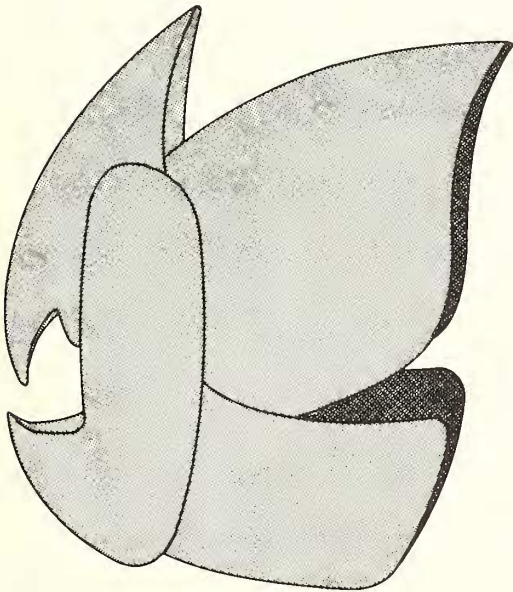
TEXT-FIG. 2. Typical dibranchiate mandibles, represented by Recent *Loligo* sp. (× 5). Mandibles are composed entirely of chitin. Terminology and orientation as in text-fig. 1, except drawn in articulated position.

are covered with distinctive, closely spaced, concentric ornament, interpreted as growth lines. On the flanks of the lower mandibles these growth lines are transected by delicate, irregularly spaced radial ridges (Pl. 9, figs. 4, 10).

Calcification is restricted to the anterior portion of both mandibles (text-fig. 4). The calcified portion of the lower jaw, the conchorhynch, comprises three distinct areas: (*a*) irregular deposits of calcite on the outer surface (Pl. 9, figs. 3, 14) that are continuous with (*b*) a distinctively denticulated occlusal or oral surface (Pl. 9, figs. 6, 16), which in turn extends ventrally to form (*c*) a smooth calcareous layer on the inner anterior portion of the lower jaw (Pl. 9, fig. 5). In *N. pompilius*, the oral or occlusal surface displays a strong, T-shaped ridge, or denticle, at the apex of the mandible, with three progressively smaller parallel denticles along the outer flanks. Adjacent to these denticles a furrow extends along the full length of the occlusal surface. The inner margin of the furrow is a sharply defined ridge, which serves as a shearing or cutting edge (Pl. 9, figs. 5, 6). In contrast to *N. pompilius*, the conchorhynch of *N. macromphalus* displays a series of four highly crenulated ridges posterior to the tightly crenulated, T-shaped apical ridge. Although these denticles stand out in sharp relief, they show no evidence of breakage or wear even in large, presumably mature specimens (Pl. 9, figs. 10, 11, 15, 16). Conchorhynchs of *N.* cf. *pompilius* available to us for study are all badly worn and details are not readily distinguishable, but they are similar to those of *N. macromphalus*, in having four relatively sharp, steep denticles. The inner surface of the *Nautilus* conchorhynch varies in detail from specimen to specimen; it is generally smooth, but some display shallow, irregularly spaced dorsoventral furrows. Removal of the conchorhynch from the lower jaw exposes the anterior surface, which in both *N. pompilius* and *N. macromphalus* is distinguished by a broad median ridge tapering towards the occlusal surface; subsidiary, irregularly spaced ridges may be present on the surface of the median ridge (Pl. 10, fig. 17). In neither *N. pompilius* nor *N. macromphalus* is the distinctive chevron pattern of biserial grooves on each side of the median ridge present as in *N.* cf. *pompilius* (Pl. 10, fig. 16). This feature is characteristic of many fossil forms, including the type species *Conchorhynchus avirostris* von Schlotheim, 1820 (Pl. 10, fig. 8); see also Gaillardot's (1824) specimens (in Teichert *et al.* 1964, fig. 338, 1*c*, *f*).

EXPLANATION OF PLATE 9

Mandibles of *Nautilus pompilius* Linné, 1758. (1–6) and *Nautilus macromphalus* Sowerby, 1849 (9–16). All figures ×1 except 6, 16 (×3), and 15 (×2·5).

Figs. 1–6, *N. pompilius* (DMNH 106740) from Gingoog Bay, N. Mindanao, Philippines: 1, 2, ventral and lateral views showing rhyncholite *in situ*; 3–5, anterior, lateral, and dorsal views of lower mandible showing conchorhynch *in situ*; 6, enlarged dorsal view of conchorhynch.

Figs. 7, 8, lateral and anterior views of articulated mandibles of *N.* cf. *pompilius* (SUI 42440) from Mutremdiu Point, Belau (Palau) Islands.

Fig. 9, lateral view of buccal mass of *N. macromphalus* (SUI 35924) from Lifou, Loyalty Islands, showing mandibles covered by buccal membrane, buccal papillae encircling mouth and oesophagus extending from lower right of buccal mass.

Figs. 10–16, *N. macromphalus* (SUI 42163) from Nouméa, New Caledonia: 10, 11, 14, lateral, dorsal, and anterior views of lower mandible with conchorhynch *in situ*; 15, 16, enlarged lateral and dorsal views of conchorhynch; 12, 13, ventral and lateral views of upper mandible showing rhyncholite *in situ*.

PLATE 9
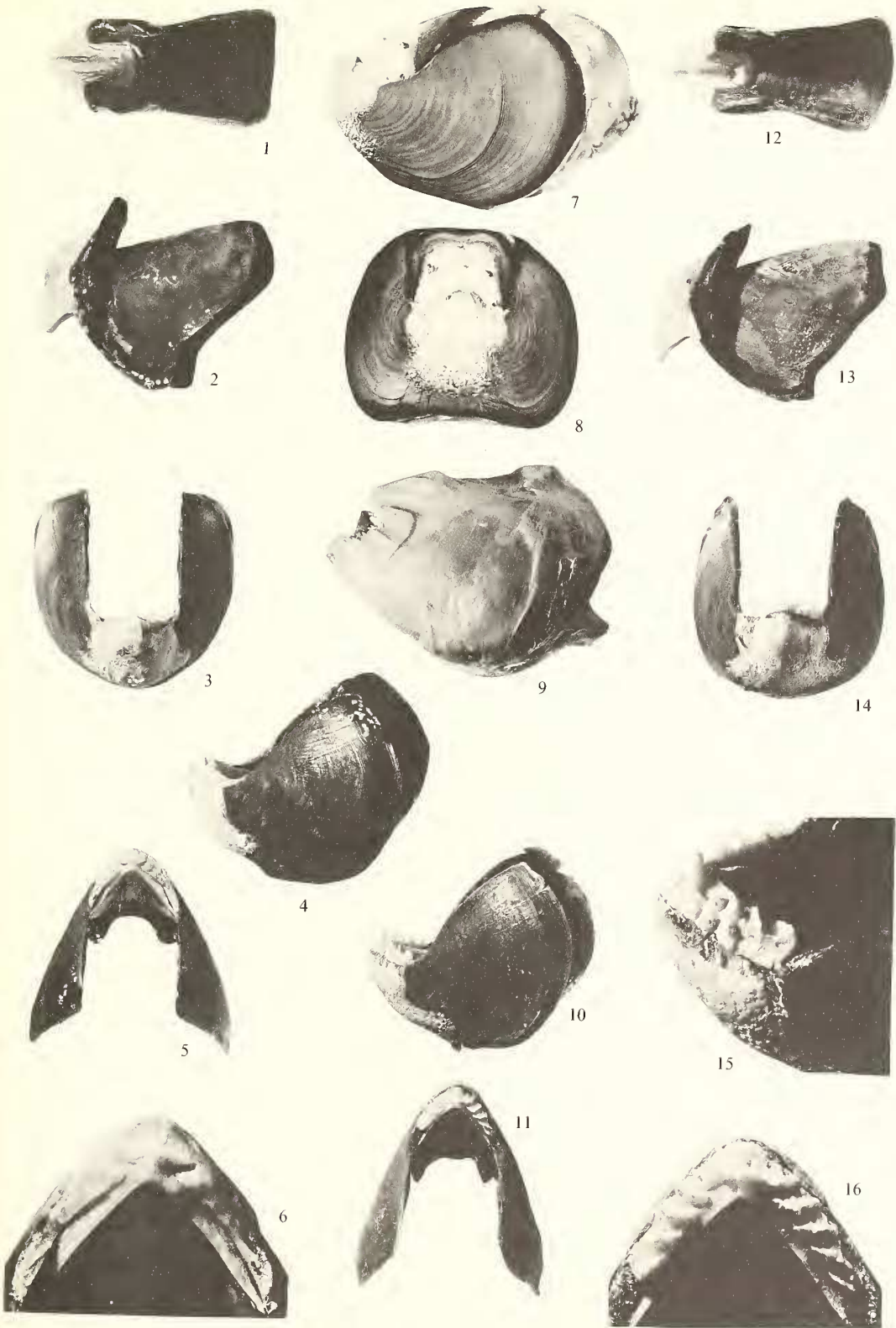
SAUNDERS *et al*, *Nautilus* jaw apparatus
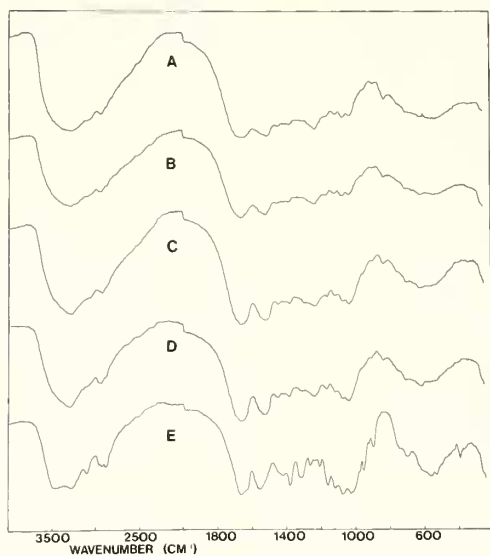
TEXT-FIG. 3. Infra-red absorption spectra of flank (A) and occlusal surface (B) of lower mandible of *Nautilus pompilius* and of occlusal surface (C) and flank (D) of lower mandible of *Loligo* sp., compared to (E) commercial chitin (from Matheson Coleman and Bell, lot P9013 CX688). Infra-red absorption spectra were obtained using a Perkin-Elmer Model 467 spectrophotometer, with samples ground and dispersed in solid potassium bromide pellets.
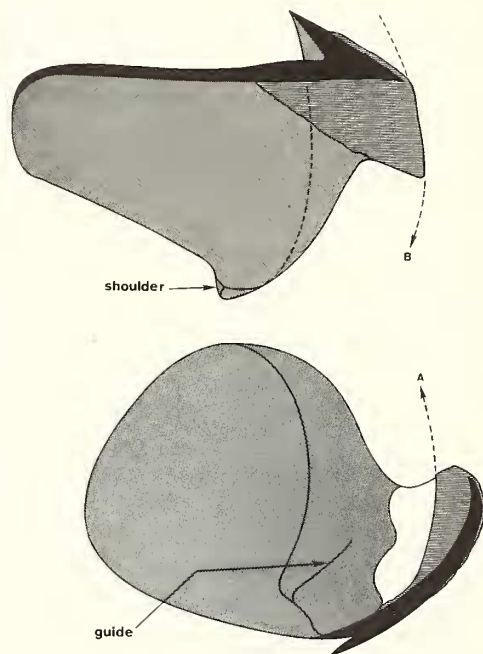
TEXT-FIG. 4. Schematic longitudinal cross sections of disarticulated upper and lower mandibles of *Nautilus pompilius* (× 1·75). Stippled areas represent unsectioned chitinous jaw and black represents sectioned portion of the same. White represents unsectioned calcareous conchorhynch; horizontally ruled areas represent sectioned calcareous rhyncholite and conchorhynch. During articulation, upper jaw is maintained tightly enclosed within lower jaw; *shoulder* of upper jaw is supported by and moves along *guide* of lower jaw, rhyncholite axis B is moved tightly against conchorhynch axis A, generating strong shearing effect.

The rhyncholite is the arrow-shaped counterpart to the conchorhynch. As a result of numerous studies based on isolated fossil specimens (for example, Gasiorowski 1973; Dieni 1975), the morphology and terminology of rhyncholites is well established (text-fig. 5). When *in situ*, the convex side of the rhyncholite shaft is located within the folded anterior edge of the upper jaw (Pl. 9, figs. 1, 12). The prominent, triangular hood projects ventrally from the jaw and serves as the upper counterpart of the inner cutting edge of the conchorhynch (text-fig. 4). The calcitic deposits of the hood extend over the edge and partially cover the anterior surface of the upper jaw; the exposed inner surface of the rhyncholite displays a prominent median ridge flanked laterally by depressions and in many specimens the inner surface of the shaft exhibits a series of longitudinal grooves, which vary in length and spacing (Pl. 10, figs. 2–5). There is considerable intraspecific variation in rhyncholite sculpture and proportions, as well as a high degree of overlap in the morphology of rhyncholites belonging to different extant species of *Nautilus* (text-fig. 6).

In mature specimens of *N. pompilius*, *N.* cf. *pompilius*, and *N. macromphalus*, the radula is a prominent, elongate, chitinous, ribbon approximately 10 mm wide and 30 mm long. The surface of the radula is covered by rows of 'teeth'; each row contains thirteen elements, consisting of two lateral and two median teeth and two median support plates distributed symmetrically on either side of the central tooth. The morphology of the various radula elements was well described by Griffin (1900), and the elements have been excellently illustrated by Solem and Richardson (1975). It should be noted that the radulae of these three species do not appear to be distinguishable in any respect.
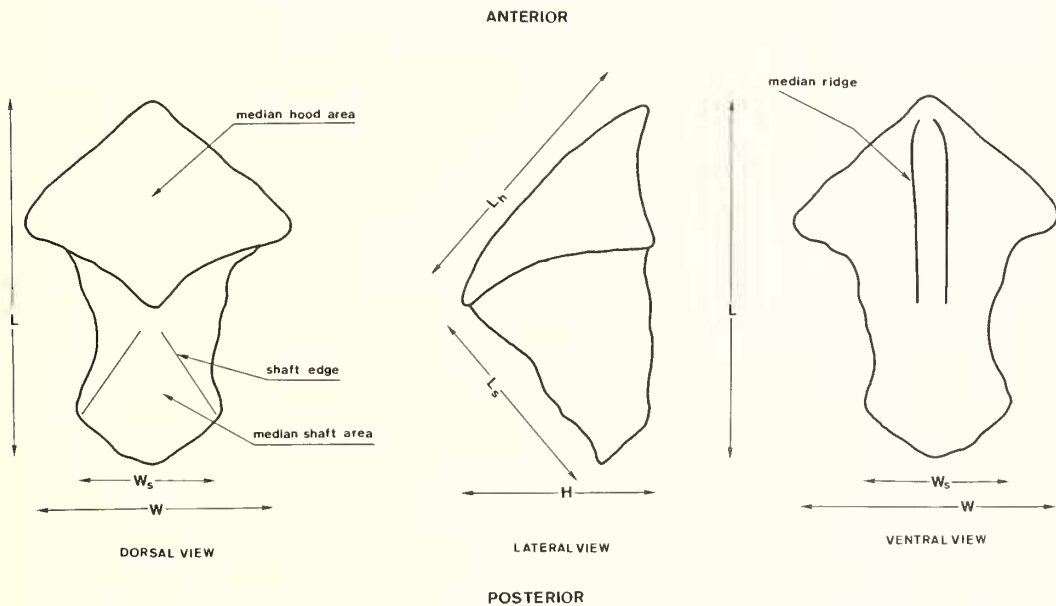
TEXT-FIG. 5. Rhyncholite dimensions, terminology, and orientation. H, rhyncholite height; L, rhyncholite length; W, maximum rhyncholite width; L_h, hood length; L_s, shaft length; W_s, shaft width.

Functional morphology

Viewed as a whole, the nautiloid jaw apparatus is admirably constructed as an efficient, extremely strong device for grasping, piercing, and shearing. The mandibles are articulated so that the upper, rhyncholite-bearing jaw fits within the lower conchorhynch-bearing jaw and the sharp, triangular rhyncholite functions as an incisor, which closes smoothly against the inner cutting edge of the conchorhynch. Powered by the numerous buccal muscles, this produces an extremely strong shearing action. The prominent denticles on the outer (anterior) edge of the conchorhynch are not masticatory, since the occlusal surfaces of the upper and lower jaws are not in direct contact, but they probably aid in grasping and facilitate shearing.
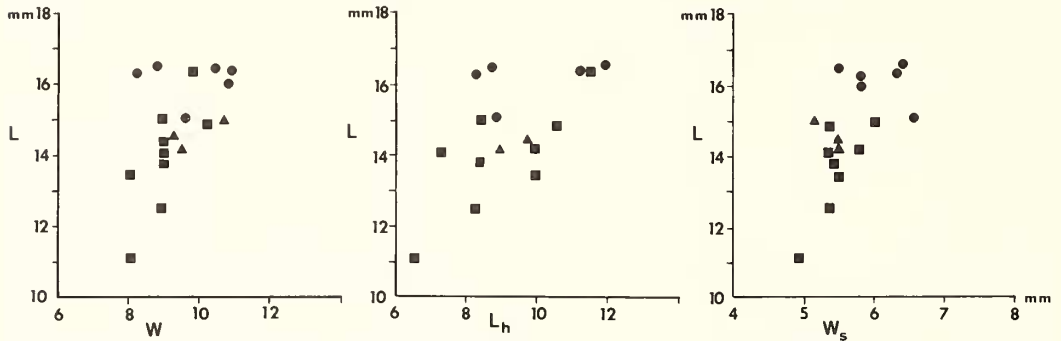
TEXT-FIG. 6. Scattergram plots of rhyncholite length (L) and width (W); length (L) and length of hood (L_h); length (L) and width of shaft (W_s). Dots represent rhyncholites from *Nautilus* cf. *pompilius*, triangles represent those from *N. macromphalus*, and squares represent those from *N. pompilius*. Note high degree of intraspecific variation and overlap between species.

Fossil and Recent rhyncholites and conchorhynchs.

Figs. 1, 20, *Syrionautilus libanoticus* (Foord and Crick, 1890) (BMNH 83663) from the Upper Cretaceous, Sahil Alma, Lebanon: 1, enlarged view of rhyncholite ($\times 4$); 20, rhyncholite in living chamber surrounded by probable remains (dark) of upper mandible ($\times 1$).

Figs. 2–5 (inner views), 7–10 (outer views), 12–15 (lateral views), rhyncholites of *Nautilus pompilius* Linné, 1758 (SUI 42423–42426) from Tañon Strait, Negros, Philippines ($\times 2.5$).

Figs. 6, 11, outer and inner views of *Rhyncolites hirundo* Biguet, 1819 (BMNH 83943b) from the Middle Triassic, Muschelkalk, Bavaria ($\times 2$).

Fig. 16, posterior view of lower mandible of *N.* cf. *pompilius* Linné, 1758 (SUI 42441) from Mutremdiu Point, Belau (Palau) Islands, with conchorhynch removed showing chevron pattern of biserial grooves on anterior conchorhynch surface ($\times 2.5$).

Fig. 17 (SUI 42432), view of lower mandible of *N. pompilius* from same locality as previous with conchorhynch removed ($\times 1.5$).

Figs. 18, 21, anterior and dorsal views of *Conchorhynchus avirostris* (von Schlotheim) 1820 (BMNH 83493b) from same locality as previous ($\times 2$).

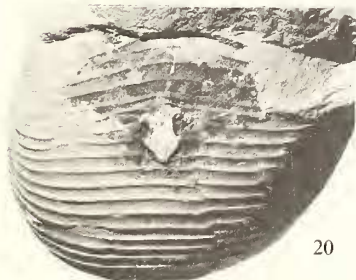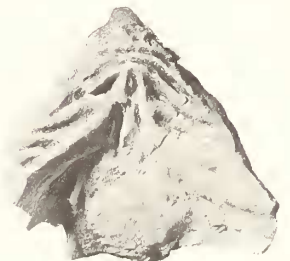Fig. 19, dorsal view of *N. pompilius* conchorhynch (SUI 42433) ($\times 2$).

PLATE 10

The striking differences between the conchorhynchs of *N. pompilius*, *N. macromphalus*, and *N.* cf. *pompilius* have been described. While the functional implications of these differences are not entirely clear, a few conclusions may be made. The delicate, high-relief denticles present in the two specimens of *N. macromphalus* examined would not withstand heavy use, for example, as would be required in shell breaking and they show no evidence of wear (Pl. 9, figs. 15, 16). In contrast, most of the conchorhynchs and, to a lesser extent, the rhyncholites of *N. pompilius* and *N.* cf. *pompilius* examined show considerable wear. In several mature specimens of *N.* cf. *pompilius*, the conchorhynch has been completely worn away in places, exposing the underlying chitinous jaw, which also demonstrates conspicuous abrasions. Such signs of wear might result from a diet richer in hard or shelled foods. Unfortunately, practically no data are available regarding the actual diet of species of *Nautilus*. Observations consist primarily of comments regarding bait used in trapping *Nautilus*; various meats, including chicken (hardly natural fare, but, nevertheless an apparent favourite), fish, molluscs, and crustaceans (Griffin 1900; Dean 1901; Willey 1902; Haven 1972; D. Faulkner and P. Ward, personal communications 1976). Additionally, Griffin noted (1900, p. 159) that the crops of *N. pompilius* which he dissected (caught in chicken-baited traps) were often filled with chicken, including feathers and sheared bones. Haven (1972, p. 79) remarked that crop content consisted of bitten pieces of bait approximately 5 mm square and occasional fragments of decapod crustacean carapaces. It also appears that the jaws may be employed effectively in fighting, judging from injuries to the hood and shell which a young male *N. pompilius* suffered while caged with other males (Haven 1972, p. 79). This might be an explanation for many of the crescentic breaks commonly observed in both extant and fossil cephalopod shells.

The exact function of the nautiloid radula is not known. However, the fact that it has been retained as such a prominent structure for so long indicates its usefulness. Griffin (1900, p. 160) concluded that the radula might be used in seizing prey and as an aid in moving food into the oesophagus. This view was supported and enlarged upon by Solem and Richardson (1975). It seems that the radula could also be used in a rasping fashion against material held in place by the jaws. This might account for the finely particulate nature of food material observed in the mouth and imbedded in the radula of several of the animals dissected during the course of this study.

PALAEONTOLOGIC IMPLICATIONS

In the present paper, utilization of the term 'rhyncholite' applies only to the calcified portion of the upper mandibles found in Recent *Nautilus* and to fossil structures closely resembling them. These rhyncholites are the forms which Till (1907) referred to as '*Nautilus-Schnäbel*' and which Teichert *et al.* (1964) assigned to the genus *Rhyncolite* Biguet. This form genus was later corrected to *Rhyncolites* by Ward and Cooper (1972), by Teichert and Stanley (1975), and by Dieni (1975). The calcified elements which develop on the lower mandibles of *Nautilus* are herein referred to as conchorhynchs. Fossil conchorhynchs have been placed in the form genus *Conchorhynchus* de Blainville (Teichert *et al.* 1964). The vernacular term 'rhyncholites' has also been applied in a general sense to a large variety of fossil forms which bear no close

taxonomic relationship to *Rhyncholites* or *Conchorhynchus* and which were grouped as '*Nicht-Nautilus-Schnäbel*' by Till (1907). These latter forms are not being considered here.

The general morphology of rhyncholites (as restricted herein) has remained remarkably stable since the Middle Triassic. This is exemplified by comparison of Recent *Nautilus* rhyncholites with those of Upper Cretaceous *Syrionautilus libanoticus* and to Middle Triassic specimens generally assigned to *R. hirundo* (Pl. 10). If encountered as isolated fossil elements, these forms would certainly be regarded as congeneric. Somewhat similar conservatism is shown by conchorhynchs; modern *Nautilus* conchorhynchs show considerable variation in detail, but basically the same morphology is represented by fossils as far back as the Middle Triassic, for example, *C. avirostris* (Pl. 10, figs. 18, 21). There have been many variations in the basic rhyncholite-conchorhynch plan, exemplified by numerous fossil rhyncholite form genera, distinguished by such criteria as proportions of hood, shaft form, curvature, etc. (see Teichert *et al.* 1964; Gasiorowski 1973). The lack of change in the basic form of these nautiloid jaw elements, in contrast to the rapid evolution and diversification of the shells of post-Triassic nautiloid genera, seems an unusually clear example of mosaic evolution.

In view of the close structural similarity between the modern and fossil cephalopod jaw apparatus, there is no reason to assume major differences in the jaw function of fossil versus modern counterparts. Thus, we reject portrayals of the rhyncholite-conchorhynch apparatus as a mechanism for grinding, with the ventral surface of the rhyncholite directly opposing the dorsal (oral) surface of the conchorhynch (see Rutte 1962; Teichert *et al.* 1964, fig. 340). Such interpretations are inconsistent with the known articulation, musculature, and operation of the jaw apparatus of *Nautilus*, as well as with the jaws of modern dibranchiate cephalopods and articulated fossil jaws.

The general similarity of fossil rhyncholites to those of modern *Nautilus* focuses on a taxonomic problem cited briefly by Teichert and Stanley (1975); isolated fossil rhyncholites and conchorhynchs which are indistinguishable from jaws of modern *Nautilus* may, according to rules of nomenclature, be regarded as synonyms of *Nautilus*. This is complicated by the fact that the only known fossil rhyncholite which occurs *in situ*, that of Cretaceous *S. libanoticus* (Foord and Crick, 1890) is also indistinguishable from *Nautilus* rhyncholites (Pl. 10, figs. 1, 2), although the shell form of the fossil species is quite different (Pl. 10, fig. 20). This demonstrates the practical need for utilizing a dual system of binomial nomenclature for the cephalopod jaw apparatus. We recommend retaining the present parataxial system as it has been developed, except in cases where identity of separate parts can be clearly established, as in *Nautilus* and *Syrionautilus*.

It is extremely difficult to establish the taxonomic affinity of most fossil cephalopod jaws, since they are only rarely found either *in situ* in the living chamber or associated with identifiable conch remains. There is only one unequivocal occurrence of fossil rhyncholites *in situ*: five specimens of *S. libanoticus* (Foord and Crick, 1890) from the Upper Cretaceous of Lebanon display the rhyncholite and, in some cases, remains of the chitinous jaw in the living chamber (Pl. 10, figs. 1, 20; also Foord 1891, figs. 67, 82; Teichert *et al.* 1964, fig. 343; Kummel 1964, fig. 334–1). Numerous mandible

associations have been reported in Mesozoic ammonites (for example, Lehmann 1970, 1971, 1972; Schmidt-Effing 1972; Dagys and Dagys 1975); Carboniferous goniatites with mandibles and radulae were described by Closs (1967*a*, *b*) from Uruguay, and Saunders and Spinosa (1974 and unpublished) have found Mississippian, Pennsylvanian, and Permian ammonoids with mandibles in the living chambers. It is notable that in only one of the mandible-ammonoid associations cited above (Schmidt-Effing 1972) is a calcified mandibular element (conchorhynch) represented and that the uncalcified mandibles inferred to belong to ammonoids resemble more closely mandibles of modern dibranchiates than those of *Nautilus*.

The known geologic range of rhyncholites and conchorhynchs, based on isolated elements, is Middle Triassic to Recent (see Gasiorowski 1973, for detailed discussion). They are not known from the Upper Triassic, a time of major nautiloid extinction, but they are relatively abundant and diverse in the Jurassic and the Cretaceous. Although widely distributed, they are relatively rare in post-Cretaceous strata. The rhyncholite-conchorhynch range corresponds quite closely to that of the superfamily Nautilaceae. This group includes the Nautilidae and five other families of involute, compressed forms with central or dorsal siphuncle and straight to sinuous sutures (Kummel 1964). The Nautilaceae are known from the genus *Cenoceras* in the Upper Triassic and are thought to have developed from the Syringonautilidae, which became extinct in the Late Triassic (Kummel 1953). The nautilaceans achieved wide distribution and diversity during the Middle and Late Jurassic, they were abundant during the Cretaceous and Early Tertiary, but in the Late Tertiary diminished to the present single surviving genus.

While it cannot be proven directly that rhyncholites and conchorhynchs are an exclusive nautilid feature, the circumstantial implications, including rhyncholite-conchorhynch associations, their geologic range, their analogy to extant *Nautilus*, as well as the occurrence and contrasting uncalcified forms of ammonoid jaws, seem conclusive. It is tempting to extend speculation, to consider whether jaw calcification may have been a factor in the survival of *Nautilus*, which may be characterized as a relatively slow-swimming scavenger-predator somewhat removed from competition with the highly developed, agile dibranchiates and fishes. However, such speculation requires additional knowledge regarding the ecology and mode of life of *Nautilus*.

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